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Effect of conspecific adult plants on the spatial patterns of the soil seed bank of *Calligonum rubicundum*

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Deterministic functions that aim at quantifying and modelling the spatial effects of shrubs on the soil seed bank of a *Calligonum rubicundum* stand are described. The procedure utilises data on the spatial location of 99 individual *C. rubicundum* plants and the number of seeds of this species in the soil at 169 grid-nodes. We developed a regression equation that quantified the effects of shrub size, shrub height and prevailing wind direction on seed dispersal. The deterministic models revealed a good fit between the measured and simulated data using parameters estimated from the data set of soil seed bank values. The results presented in this paper provide a way to examine, quantify and model the spatial effects of shrubs on soil seed banks at the stand level. The method presented here can be applied to examine and estimate the influence of dominant plants on other biotic or abiotic properties of an ecosystem.

Introduction

Environmental heterogeneity due to abiotic or biotic properties and spatial plant interactions are important factors in establishing and forming the structure of plant communities or populations in general (Odum 1969, Webb and Willson 1985, Legendre and Fortin 1989, Benton and Grant 1996, Larson 1999, Wijesinghe and Hutchings 1999). Ecological theory has recently emphasised the effects of plant individuals as a source of patterns of communities or populations (Zinke 1962, Glenn-Lewin 1980, Wada and Ribbens 1997, Kuuluvainen and Linkosalo 1998, Tang *et al*. 1999). This so-called individual-based analysis of ecological problems is derived from the relationships among the components of the system (Zinke 1962, Thompson and Grime 1979, Ellner and Shmida 1984, Grice and Westoby 1987, Fowler 1988, Silvertown and Smith 1989, Philippi 1993, Thiede and Augspurger 1996, Wada and Ribbens 1997). There is indeed evidence that individual scale may strongly affect desert vegetation dynamics and community composition (McGraw 1987, Kuuluvainen and Pukkala 1989, Milton 1995, Wang and Liang 1995, Benton and Grant 1996, Wada and Ribbens 1997, Larson 1999, Tang *et al*. 1999). When implementing this individual-based approach, computer regression analysis and simulations have often been used to derive significant models or functions (Zinke 1962, Cohen 1966, Milton 1995, Wada and Ribbens 1997, Kuuluvainen and Linkosalo 1998, Giedeman 1999, Wang and Liang 1995).

In most desert ecosystems, shrubs are the most important ecosystem component, because they have a dominant influence on ecosystem organisation and function (Ellner and Shmida 1981, 1984, Boyd and Brum 1982, Grice and Westoby 1987, Philippi 1993, Milton 1995, Wang and Liang 1995, Guo *et al*. 1999). The effects of shrubs on the observed spatial patterns of desert ecosystems are due to multiple influences, increasing their role in intercepting precipitation, taking up water and nutrients by their roots, resource island development, seed dispersal patterns and soil seed bank distribution (Ellner and Shmida 1981, 1984, Philippi 1993, Milton 1995, Wang and Liang 1995).

A model of plant individual influences based on ecological field theory (EFT) (Wu *et al*. 1985) has been applied to spatially explicit ecosystem interactions between biotic components of ecosystems. The outcome of ecosystem interactions was described directly without explicit consideration of resource distribution. Often the form of plant influence has then been tested against empirical observations (Kuuluvainen and Pukkala 1989, Kuuluvainen and Linkosalo 1998, Escudero *et al*. 1999).

Thus far, models describing the distance-dependent or size-dependent influences of individual plants on ecosystem properties have been derived mostly from theoretical considerations (Wu *et al*. 1985, Walker *et al*. 1989, Mou *et al*. 1993). The reason is that it is very problematic to separate the effects of individual plants because the

influence domains of plants overlap in structurally complex plant stands. However, the derivation of models expressing the influence of a single plant is not too difficult. For example, the following is a plant influence function (PIF):

$$f_d(s) = a_d + b_d s c_d \quad (1)$$

where f is the effect of a plant, s is the distance between two plants, a_d, b_d and c_d are estimated parameters, and d denotes the size of a plant (Kuuluvainen and Linkosalo 1998). Two other forms of the plant influence function have been widely used to describe the abiotic and biotic properties of an ecosystem. One encompasses the negative exponential models:

$$y = ae^{-bx} \quad \text{(Laman 1996)} \quad (2)$$

or

$$g(s) = g_0 \exp(-bs^2) \quad \text{(Kuuluvainen and Linkosalo 1998)} \quad (3)$$

The other form often used is the inverse power law:

$$y = ax^{-b} \quad \text{(Laman 1996)} \quad (4)$$

where y is the density of seed resource, x is the distance from the plant, a and b are the estimated parameters.

When considering a stand of shrubs, it is logical to assume that at any given point in the ecosystem space, the combined spatial influences of multiple surrounding shrubs determine both abiotic and biotic properties at that point (Kuuluvainen and Linkosalo 1998). These basic approaches were used to derive the combined effect of multiple surrounding plants, the Combined Plant Influence (CPI), at a location in a stand. The first case has a variable with a known minimum value (zero), but no *a priori* defined upper limit of range. Examples of this kind of variable include humus thickness (Angelina *et al*. 1999), soil moisture, density of seed rain or soil seed bank (Bustamante and Simonetti 2000, Cabin and Marshall 2000). In this case, the CPI can be defined according to the following equations (Kuuluvainen and Linkosalo 1998):

$$F_d(p) = \sum_{i \in I_p} f_d(s(i)) \quad (5)$$

$$\text{or } Ss = \Sigma H_i ((\cos\alpha_i + 1)/2) / d_i \quad (\text{slope} > 15°) \quad (6)$$

$$= \Sigma (H_i/2) / d_i \quad (\text{slope} < 15°)$$

(Escudero *et al*. 1999) (7)

where I_p is the influence vicinity that includes plants i from a point p in the stand, H is the height of each plant, d_i is its distance to a point, α is the angle between the direction of prevailing wind and the line linking the plant to the point.

The second case has a variable with an *a priori* defined variation range that is, or can be, scaled between 0 and 1. An example of this kind of variable is the fraction of sky covered by the canopy. Depending on the original definition of plant effect, i.e. either increasing or decreasing with distance from a plant, the following equations can be used:

$$F_d = 1 - \prod_{i \in I_p} [1 - f_d(s(i))] \quad (8)$$

$$F_d = \prod_{i \in I_p} f_d(s(i)) \quad (9)$$

The multiplication includes plants i that are in the influence vicinity I_p from a point p in the stand (Kuuluvainen and Linkosalo 1998).

Natural desert ecosystems are considered to be among the most threatened habitats in arid areas of north-western China. Shrubs play a key role in the stability of natural and artificial desert ecosystems in China, and *C. rubicundum* is one of the most important dominant shrubs. However, the soil seed bank pattern of *C. rubicundum* has not been studied. In this paper, we use field empirical data to model the spatial Combined Plant Influence (CPI) of individual plants on the soil seed bank at any given point in a *C. rubicundum* population stand. Seeds of *C. rubicundum* are large and winged, and their dispersal is sensitive to wind and plant height. Information is needed on the distribution pattern of soil seed banks of *C. rubicundum* to better understand the spatial distribution pattern and succession of *C. rubicundum* populations.

Materials and Methods

Study site and measurement

This study was carried out at the edge of Zhungger desert in China, approximately 12km north of Habahe county in Xingjing Ugur Autonomous Region (48°18'N, 86°30'E, 654m asl). The climate is arid, with mean annual rainfall of 155mm, wind velocity of 4.3m s^{-1} with prevailing wind from the north-west (data from Habahe meteorological station). The experimental site was 1 600m^2 and located on sandy substrate. *C. rubicundum* is the dominant species and widely distributed in this region. The herbaceous layer is composed of *Climacoptera brachiata, Ceratocarpus arenarius, Petrosimonia sibirica, Kochia scoparia* and *Agriophyllum arenarium*, among others.

Sampling design

A 40m x 40m square was laid out, with one side perpendicular to the prevailing wind direction. It was regularly divided every 2m to give a grid of 441 nodes and 400 subquadrats. Every mature plant of *C. rubicundum* was identified and located by subquadrats (Figure 1).

To estimate the influence of mature plants on soil seed banks, the canopy size and plant height of every individual was measured. We sampled the 169 grid-nodes located in the middle of the study quadrat from line 8 to line 32 (Figure 1), collecting one soil sample 40cm x 40cm, 5cm deep. The *C. rubicundum* seeds in each soil sample were identified and counted. Ninety-nine mature *C. rubicundum* plants were detected in the study quadrat.

All mature individuals could influence the soil seed bank at any given point in the shrub stand. This plant influence is likely to depend on distance between each mature individual and the given point, and plant size, e.g. height or canopy size. In this desert shrub population, this influence increases with accretion of size of plant and reduction of distance between a plant and a given point. In order to analyse the vicinity of influence of mature plants on the soil seed bank, we compared neighbourhoods of radius 2H, 3H, 4H and 5H

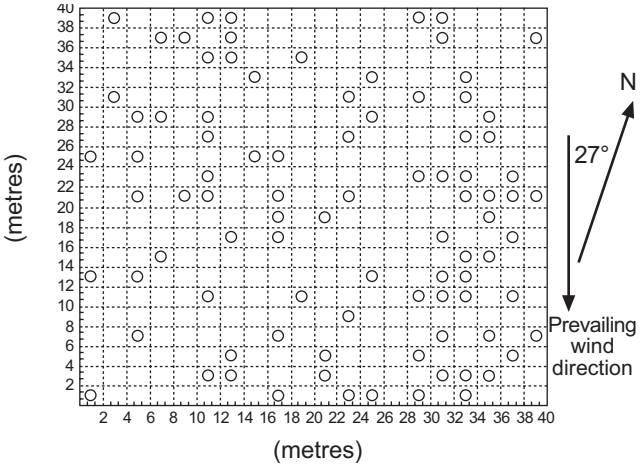

Figure 1: The location of *Calligonum rubicundum* individuals in the study quadrat with azimuth

(H being the average height of all mature individuals in the study quadrat). Simple linear regression analyses were performed between soil seed banks (*S*) and number of selected mature individuals (*I*), and summation of height (*H*) and canopy (*C*) based on different radii using the STATISTICA software package (Statsoft 1993).

Results

The influence of shrubs on the soil seed bank

All linear regression equations between the soil seed bank and summations of height and canopy of selected mature individuals were significant (Figures 2, 3 and 4). These results suggest that the optimal R must be based on a consideration of the selected individual and summation of height and canopy. As the correlations among number of selected individuals and summations of height and canopy were highly significant ($P < 0.0001$), we can consider only one factor in determining the radius of the selected circle.

Spatial patterns of soil seed bank

The general spatial pattern of soil seed banks for a *C. rubicundum* stand is portrayed in Figure 5, which depicts density contours determined from the 169 sampled grid-node surveys. The strong influence of number, location, height and canopy of shrub individuals is evident in the spatial pattern of the soil seed bank. A wind-dispersed effect is not evident from Figure 5, possibly because the distance between sample points was too large and soil seed bank data did not express the wind effect.

Function of combined shrub influence on soil seed banks

The following form of shrub influence function on soil seed banks was chosen for the simulation model:

$$S_d = a_0 + a_1 \Sigma H_i ((\cos\alpha_i + 1)/2) / d_i + a_2 \Sigma C_i ((\cos\alpha_i + 1)/2) / d_i \quad (10)$$

where S_d is the density of soil seed, H_i is the height of selected mature plant (i), α_i is the angle between prevailing wind direction and the line linking the plant (i) to the sampled grid-node, d_i is the distance between plant and node, and a_0, a_1 and a_2 are estimated parameters.

Equation 10 evaluates the seed-supplying efficiency of mature plants and the effect of wind. The coefficient multiplying the height ranges from 0 when the mature selected plants are located downwind of the sampled nodes ($\alpha = 180°$) to 1 when they are upwind of nodes ($\alpha = 0°$ or $\alpha = 360°$). Mature plants located upwind of sampled nodes must be more efficient seed sources than those located downwind (wind effects).

A multiple regression approach was applied to determine three parameters (a_0, a_1 and a_2). The variables were determined on the basis of information of summation of height and canopy because the influence of any given point in the stand on the soil seed bank can be made by incorporating several selected individual plants.

Model of soil seed bank and testing

In the study quadrat, all individual plants and sampled grid-nodes were located so that the angle between the prevailing wind direction and the line linking the plant to the sampled grid-nodes (α_i), and the distance between the plant and sampled node (d_i), could be obtained using analytic geometry. We applied $\sum H_i ((\cos\alpha_i + 1)/2) / d_i$ and $\sum C_i((\cos\alpha_i + 1)/2) / d_i$ as independent variables (*V1, V2*), and the following shrub influence model for soil seed bank was derived by the method of multiple regression based on Equation 10.

When R is 2H:

$$S_d = 27.0625 - 3.4377 \sum H_i ((\cos\alpha_i + 1)/2) / d_i + 4.9805 \sum C_i((\cos\alpha_i + 1)/2) / d_i \quad (11)$$

($r^2 = 0.2123$, $P < 0.0218$, $F_{(2,166)} = 3.9177$)

When R is 3H:

$$S_d = 24.5837 - 8.7064 \sum H_i ((\cos\alpha_i + 1)/2) / d_i + 7.1927 \sum C_i((\cos\alpha_i + 1)/2) / d_i \quad (12)$$

($r^2 = 0.2608$, $P < 0.0030$, $F_{(2,166)} = 6.0314$)

When R is 4H:

$$S_d = 22.4152 - 11.0469 \sum H_i((\cos\alpha_i + 1)/2) / d_i + 8.4153 \sum C_i((\cos\alpha_i + 1)/2) / d_i \quad (13)$$

($r^2 = 0.3096$, $P < 0.0002$, $F_{(2,166)} = 8.8017$)

When R is 5H:

$$S_d = 20.6338 - 11.8595 \sum H_i((\cos\alpha_i + 1)/2) / d_i + 8.4139 \sum C_i((\cos\alpha_i + 1)/2) / d_i \quad (14)$$

($r^2 = 0.3347$, $P < 0.0001$, $F_{(2,166)} = 10.4700$)

The four linear regression equations are highly significant according to the radius of different selected circles. These results indicate that the influence domains of individual shrubs can be described with deterministic functions.

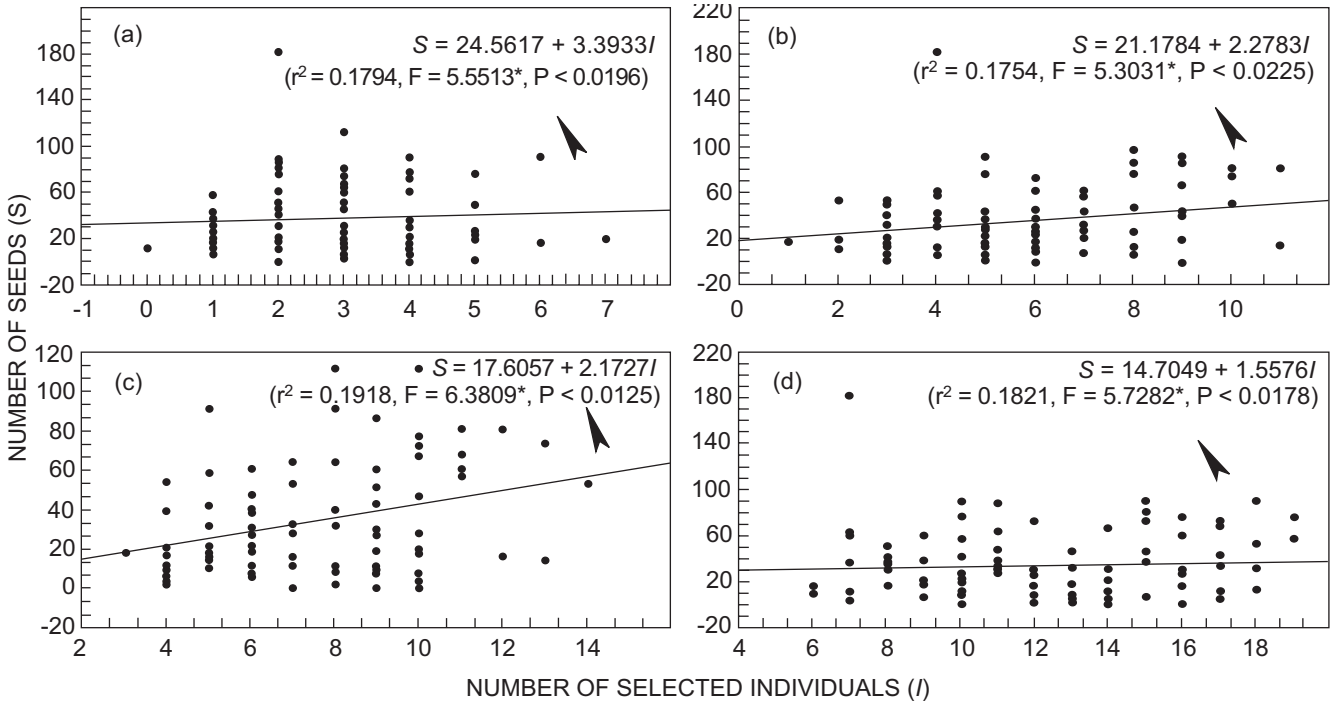

Figure 2: The relationship between soil seed bank (*S*) and number of selected mature individuals (*I*) based on different circles of all sampled grid-nodes. (a) radius(R) of selected circle is 2H; (b) R is 3H; (c) R is 4H; (d) R is 5H. The equations of linear regression and testing results are listed

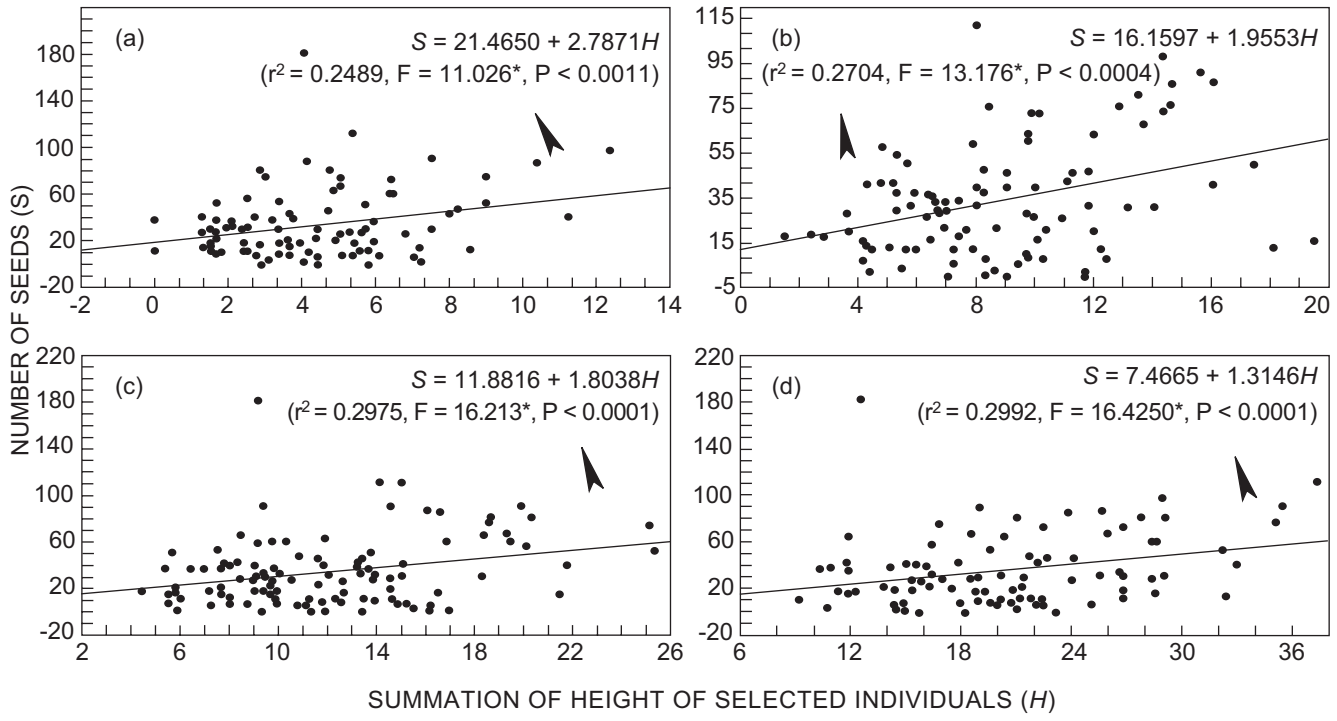

Figure 3: The relationship between soil seed bank (*S*) and summation of height of selected mature individual (*H*) based on different circles of all sampled grid-nodes. (a) R is 2H; (b) R is 3H; (c) R is 4H; (d) R is 5H. The equations of linear regression and testing results are listed

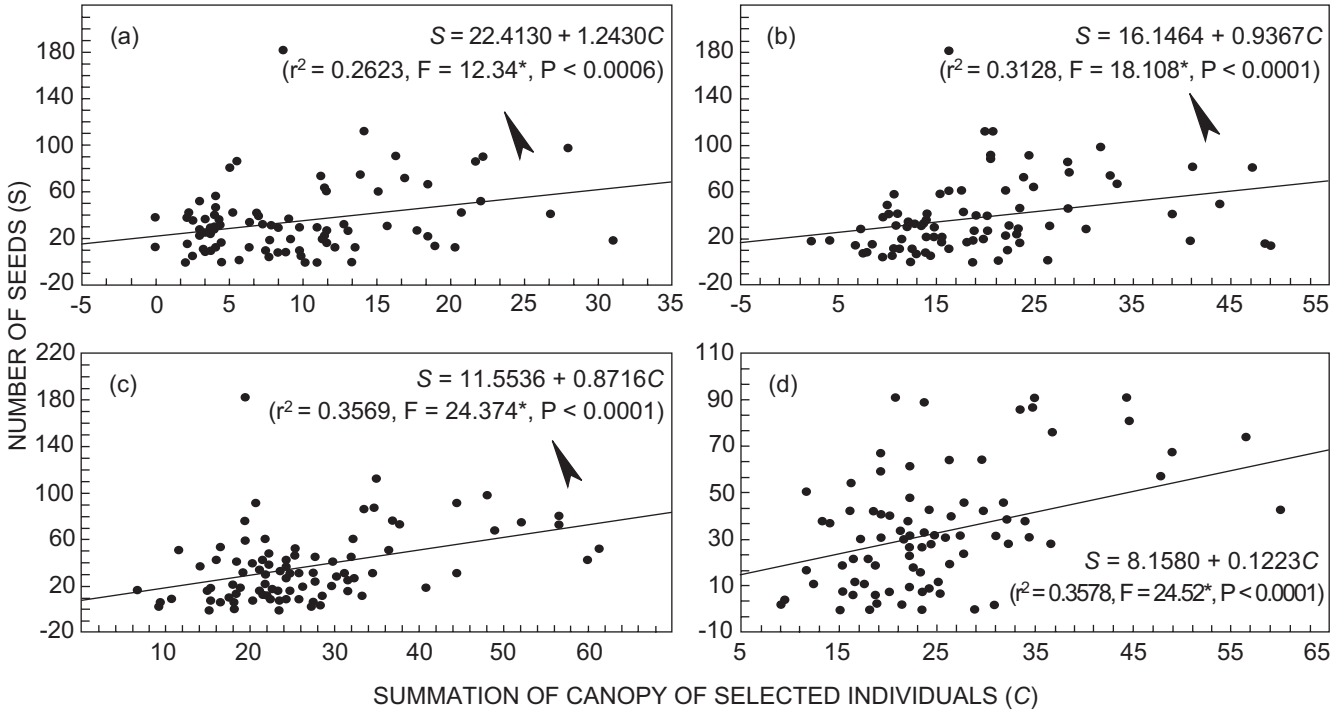

Figure 4: The relationship between soil seed bank (*S*) and summation of canopy of selected mature individuals (*C*) based on different circles of all sampled grid-nodes. (a) R is 2H; (b) R is 3H; (c) R is 4H; (d) R is 5H. The equations of linear regression and testing results are listed

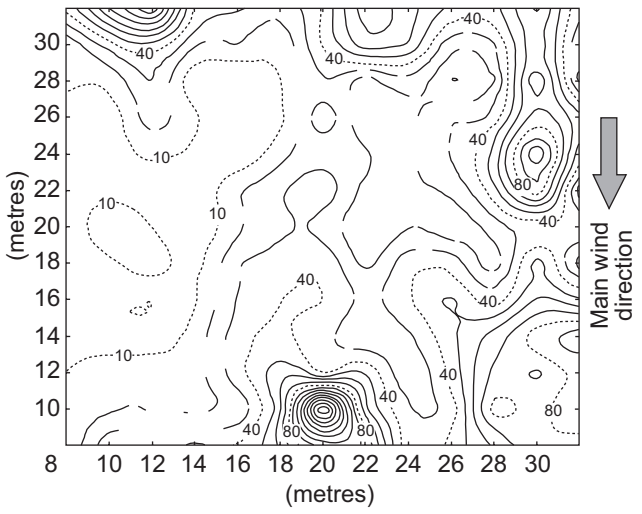

Figure 5: Density contours of the soil seed bank for *Calligonum rubicundum* population. Contour lines were generated from the density of the soil seed bank from 169 sampled grid-node surveys. The X-axis and Y-axis represent the edges of the quadrat, as portrayed in Figure 1

Discussion

In desert ecosystems, shrubs largely regulate the supply and spatial distribution of central biotic factors, such as soil seed banks. Considering plant-plant interactions, shrubs usually play a dominant role in the stability and succession of desert vegetation, and mature shrubs exert a strong influence on distribution pattern of soil seed banks (Ellner and Shmida 1981, Boyd and Brum 1982, Ellner and Shmida 1984, Milton 1995, Wang and Liang 1995, Bustamante and Simonetti 2000).

In plant ecology, the development of ecological field theory requires the building of spatially explicit and individual-based models describing plant effects on biotic components of an ecosystem (Wu *et al*. 1985). A major problem in this approach has been the very arbitrary determination of the form of the plant influence function and how to determine the plant influence on biotic and abiotic properties of an ecosystem (Zinke 1962, Kuuluvainen and Pukkala 1989, Kuuluvainen and Linkosalo 1998). In fact, the plant influence function usually has been determined *a priori* and then tested by empirical measurements (Kuuluvainen and Linkosalo 1998).

Often the effects of individual plants on ecosystem properties has been studied using isolated individuals (Glenn-Lewin 1980, Winn 1985, Kuuluvainen and Pukkala 1989, Wada and Ribbens 1997, Kuuluvainen and Linkosalo 1998, Escudero *et al*. 1999, Tang *et al*. 1999, Liu and Zhong 2000). However, results from these studies may not be applicable to plant population and community stands, because the overlapping influence of several individual plants in a stand may be qualitatively different and more complicated than those produced by isolated plants (Kuuluvainen and Pukkala 1989, Kuuluvainen and Linkosalo 1998). For example, in a desert shrub stand, the influence of individual shrubs on soil seed banks must overlap due to the wind effect, even where the individual shrubs are very sparse and unevenly distributed.

The results presented in this paper provide a way to examine, quantify and model the spatial effects of shrubs on the soil seed bank at the stand level. The method presented here can be applied to examine and estimate the influence of dominant plants on other different biotic or abiotic properties of the ecosystem.

Finally, understanding the role of individual plants in creating and maintaining environmental heterogeneity may be necessary for the understanding of succession and restoration of desert vegetation. The method presented may help to disentangle the influences of individual plants and population structural heterogeneity.

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